A SURVEY OF SEED SURFACE MORPHOLOGY IN *HESPERANTHA* (IRIDACEAE)[1]

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ABSTRACT

Seeds of a range of species of *Hesperantha* were examined with light and scanning electron microscope (SEM) and compared with three species of the most closely related genus, *Geissorhiza*. A turbinate to globose shape with a persistent funicle and a testa of uncontorted epidermal cells with smooth surfaces is apparently the basic seed type. Modifications of the basic type include increasing compression and a triangular or more or less irregular shape, sometimes accompanied by wrinkling and crumpling of the epidermal cells, and the development of dual tails and wings. This is most marked within *Hesperantha* sect. *Radiata* (but not *H. marlothii* of the section), where these modifications are accompanied by reduction in seed size. Wing-like structures are also developed within sections *Hesperantha* (*H. spicata* and *H. cedarmontana*) and *Concentrica* (*H. fibrosa*) but in both of these groups without accompanying crumpling of the epidermal cells, which coincidentally have developed rough surfaces.

Hesperantha Ker is a genus of some 55 species of corm bearing perennials of Iridaceae subfamily Ixioideae. It is centered in Southern Africa, but a few species occur in the montane areas of tropical Africa, extending as far north as Cameroon and Ethiopia. The genus has recently been revised for the winter rainfall area of South Africa by Goldblatt (1982, 1984) and is being studied in eastern Southern Africa by Hilliard and Burtt (1979, 1982). This study of seed morphology in *Hesperantha* was made in conjunction with the revisionary work, now completed or in progress.

Seed morphology of Iridaceae is in general poorly known and thus seldom has been of taxonomic value below the generic level. Differences in seeds between genera are, however, sometimes striking and may provide important generic characteristics. Good examples are the circumferentially winged seeds of *Gladiolus* and its close allies, the two winged seeds of *Watsonia*, and the inflated seeds with spongy testa of *Tritoniopsis* and *Anapalina*. This study was thus undertaken in the hope that some characteristics of taxonomic use would be found in *Hesperantha* at species and generic level. Seventeen species of *Hesperantha*, including examples from all four sections (Goldblatt, 1982), as well as three species of the related genus *Geissorhiza* Ker were assembled for light and scanning electron microscope examination. This represents a large sample for a monocot genus such as *Hesperantha*, in which seeds are typically produced after flowering and are seldom collected and consequently poorly known.

Seeds of *Hesperantha* have not previously been studied in detail, but SEM studies of seed morphology have been made in a few other genera of subfamily Ixioideae, in conjunction with the systematics notably in *Syringodea* (de Vos, 1974) and in *Crocus* (Baytop et al., 1975; Mathew, 1976). In *Crocus* some interesting seed surface features including trichomes and papillae have been found to be of taxonomic significance. In systematic studies of other genera of Ixioideae, seed morphology is occasionally of limited taxonomic use, as in *Tritonia* (de Vos, 1982: 113) where one or two species stand out from their allies in having unusual seed modifications.

The extensive study of Huber (1969) on the seed morphology of the monocotyledons deals largely with internal seed structure, and not at all with detailed surface microstructure such as is observed with the SEM. His observations on *Hesperantha* are very general and relate primarily to tribal and familial classification.

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MATERIALS AND METHODS

The seeds of 16 species of *Hesperantha* (about a third of the genus) were examined by scanning electron microscopy (SEM). Sufficient viable seeds were studied to document the variation present within each population. Four to ten seeds were generally adequate. Three additional species of the closely related genus *Geissorhiza* were also examined as out-groups in the hope that this would aid in the establishment of character polarity (Table 1). One population only of all species except *H. marlothii* was examined with the SEM. The variation in seed size in *H. marlothii* was such that two populations were studied, covering the extremes encountered in the species. Samples of several populations of *H. falcata* and *H. radiata* were also examined under the light microscope to determine whether material studied was typical of the species. In all cases they matched closely the samples studied. One more species, *H. pauciflora* (sect. *Hesperantha*) was also examined under the light microscope and since it had seeds exactly like those of *H. falcata* (also sect. *Hesperantha*), it was not examined further.

The number of populations examined may appear to be too small to gauge the variation within species but as indicated in the introduction, seed samples are difficult to obtain in *Hesperantha* in which plants are seldom collected in fruit. The material studied here therefore represents an unusually large assemblage. Where more than one population was available, as in *H. falcata* and *H. radiata*, the seed was examined with the light microscope and found to match the seed of the population studied with the SEM. Thus as far as it is possible to estimate, the single populations studied appear to be representative of the species. Several of the species examined (*H. elsiae, H. purpurea, H. brevifolia, H. cedarmontana*) are known from one or very few populations and are so restricted in their distributions that the material studied here represents a good sampling of the species. Among the widespread species, several populations were checked in *H. falcata* and *H. radiata* while only single samples were available in *H. bachmannii* and *H. pilosa*.

Viable seeds were attached with water soluble white glue to aluminum stubs, coated with 500–700 Å of gold in a sputter coater, and examined in a Hitachi S-450 SEM at 15 kV and 60–80 μA. Photomicrographs were made with Type 55 P/N Polaroid film. Contact prints were made on Illford No. 2 paper. Surface features are presented at two magnitudes of magnification: 35×–90× to show overall seed shape and surface topography, and 1,000× to resolve the microsculpture of the epidermal cell surface.

DESCRIPTION OF SEED FEATURES

The variation in the seeds of *Hesperantha* species is often limited to relatively minor modifications that produce large differences in seed shape, sometimes even within one capsule. There are, however, certain patterns of variation that appear, at least from the small samples available, to be characteristic of particular species. The variation within *Hesperantha* as well as that found in a sample of three species of the closely related genus *Geissorhiza* is presented in Figures 1–29. Only 13 of the 16 species of *Hesperantha* examined are illustrated. The additional species studied add no significant information to the observed pattern of variation. The variation is described in the following pages in sections dealing with shape, size, color, surface morphology, and microsculpturing.

Shape. The basic shape of *Hesperantha* seeds is turbinate to turbinate-globose. The embryo containing portion is globose to ovoid and this is modified to a turbinate shape by the persistent funiculus present on the seeds of many of the species (e.g., Figs. 1, 3, 5, 8). The same basic shape is evident in *Geissorhiza* (Figs. 16, 17). The more regular globose shape, illustrated here by *H. erecta* (sect. *Concentrica*) and *H. falcata* and *H. luticola* (both sect. *Hesperantha*) (Figs. 1, 5, 8), occurs in species of all sections of *Hesperantha* except sect. *Radiata*, as well as in *Geissorhiza* (*G. humilis*). The seed is more abruptly constricted to the persistent funiculus in these species.

The basic turbinate to globose shape is modified in a number of the species. The modifications can be grouped into three different types. An irregularly wrinkled surface occurs in several species of *Hesperantha* distributed in several sections (e.g., *H. bachmannii*, Fig. 4; *H. muirii*, Fig. 13) and in *Geissorhiza burchellii* (Fig. 18).

In contrast, seeds with irregular shape, a strongly wrinkled or crumpled surface coupled with the presence of two tails (one is the funiculus), and/or longitudinal wings characterize four of the five species of sect. *Radiata*; *H. muirii, H. elsiae* (Fig. 14), *H. radiata* (Fig. 11), and *H. brevifolia* (Fig. 12). The latter species appears to be the most specialized in this respect. These fea-

TABLE 1. Voucher information for the species of *Hesperantha* and *Geissorhiza* studied here. Species of *Hesperantha* are arranged taxonomically according to the sectional classification proposed by Goldblatt (1982). All collections are from the Cape Province, South Africa.

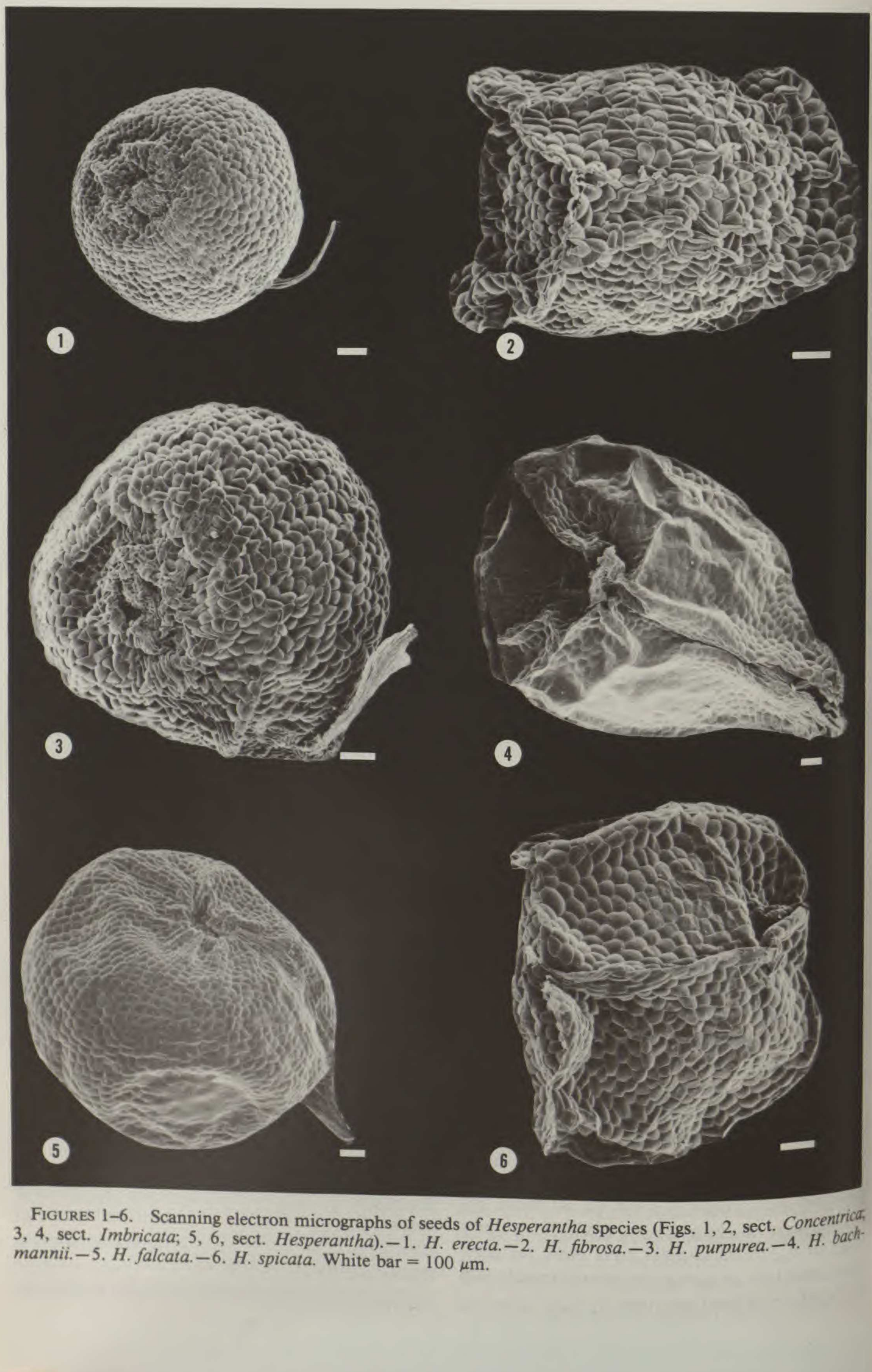
Species	Collection Data
	Hesperantha
	Sect. *Concentrica*
H. erecta (Bak.) Benth. ex Bak.	Saldanha distr., Donkergat, Posberg, *Goldblatt 4095* (MO).
H. fibrosa Bak.	Commonage S of Caledon, *Goldblatt 5899* (MO).
H. flexuosa Klatt	Wildepaardehoek Pass, *Goldblatt 5755* (MO).
H. montigena Goldbl.	Worcester distr., Mt. Brodie, *Esterhuysen 35307* (MO).
H. pilosa (L. f.) Ker	Caledon Zwartberg, *Goldblatt s.n.*, no voucher.
	Sect. *Imbricata*
H. bachmannii Bak.	N of Hankey, *Goldblatt 4937* (MO).
H. purpurea Goldbl.	Perdekraal, Calvinia distr., *Goldblatt 6246* (MO).
	Sect. *Radiata*
H. brevifolia Goldbl.	Piketberg, Zebrakop, *Esterhuysen 35320* (MO).
H. elsiae Goldbl.	Cedarberg, top of Krom River Kloof, *Goldblatt 5331* (MO).
H. marlothii Foster	Calvinia–Middelpos Rd. near Blomfontein, *Goldblatt 5813* (MO)—population 1; Nieuwoudtville escarpment, *Goldblatt 5835A* (MO)—population 2.
H. muirii (L. Bol.) Lewis	Hills W of Riversdale, *Goldblatt 5437* (MO).
H. radiata (Jacq.) Ker	N end of Cold Bokkeveld, *Goldblatt 5343* (MO).
	Sect. *Hesperantha*
H. falcata (L. f.) Ker	Bulshoek, Olifants R. Valley, *Goldblatt s.n.*, no voucher.
H. cedarmontana Goldbl.	Cedarberg, Middelberg Plateau, *Goldblatt 5130* (MO).
H. pauciflora Lewis	Kamiesberg, Welkom, *Goldblatt s.n.*, no voucher.
H. luticola Goldbl.	Calvinia–Middelpos Rd. near Blomfontein, *Goldblatt 5814* (MO).
H. spicata subsp. *graminifolia* (Sweet) Goldbl.	Cape Peninsula, near Cape Pt. Reserve, *Goldblatt 5263* (MO).
	Geissorhiza
G. burchellii Foster	Langeberg near Swellendam, *Esterhuysen 35604* (MO).
G. humilis (Thunb.) Ker	Cape Peninsula, near Cape Pt. Reserve, *Goldblatt 5263* (MO).
G. heterostyla L. Bol.	Near Humansdorp, *Goldblatt 6211* (MO).

tures are not present elsewhere in the genus. They do not, however, characterize all species of sect. *Radiata*. Population 2 of *Hesperantha marlothii* (Fig. 5) has the generalized turbinate shaped seed that is characteristic of the genus while the other population of *H. marlothii* studied has seed of a nearly pyramidal shape (Fig. 10). This is probably linked to the large seed size in this population and is presumably caused by the pressure of seed packing in the capsules. Dual tails and wings are not always present on all seeds examined (e.g., *H. elsiae*, Figs. 14, 15), but at least most seeds in each sample have these features. Again, this lack of uniformity is presumably due to the effects of seed packing.

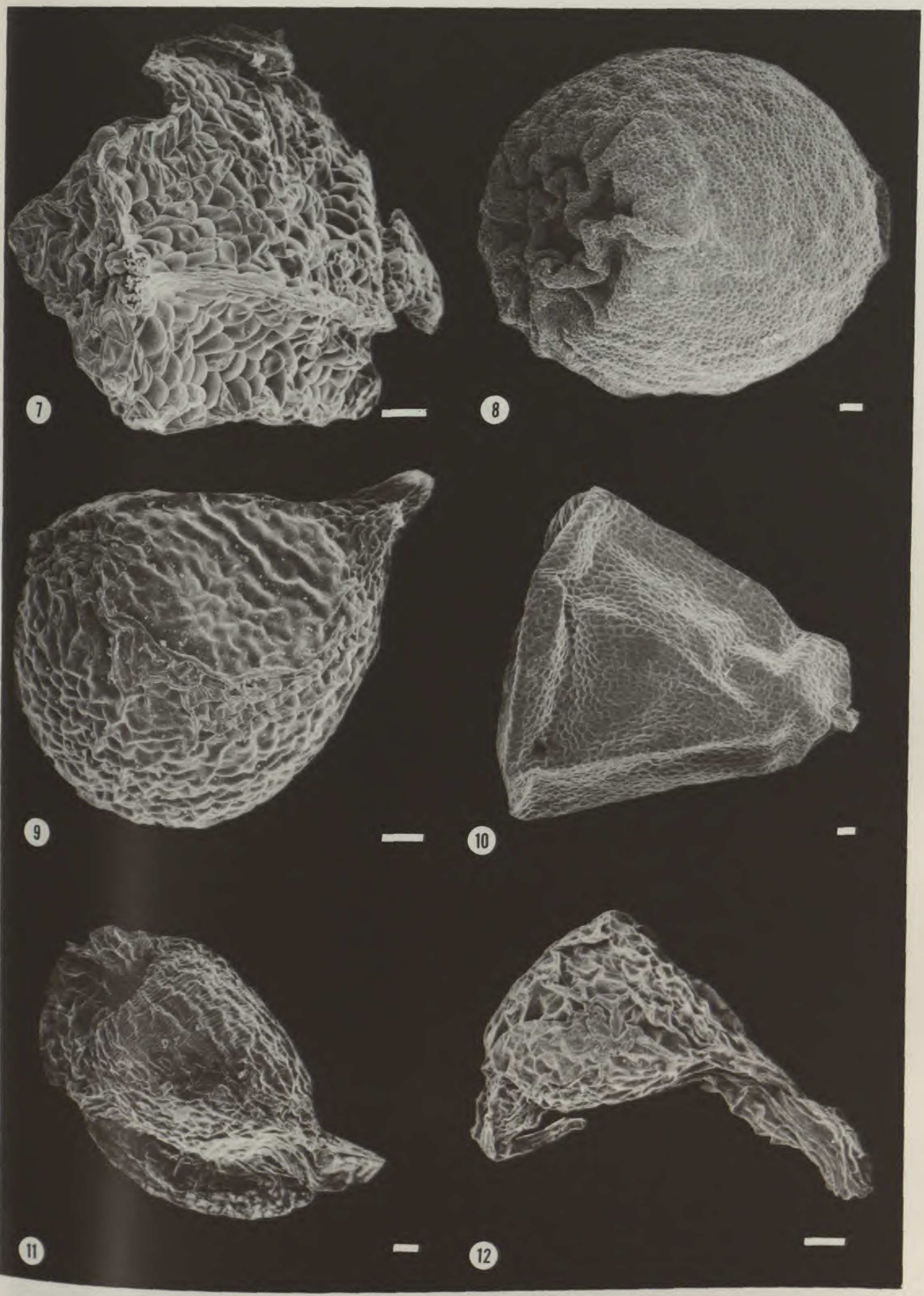
Finally, *Hesperantha fibrosa* (sect. *Concentrica*) (Fig. 2) and two species of sect. *Hesperantha*, *H. spicata* (Fig. 6) and *H. cedarmontana* (Fig. 7), have ellipsoid to irregularly shaped seeds with narrow longitudinal and apical wings and little or no contortion of the epidermal cells.

At the distal end of the raphe of many species of *Hesperantha* there is a porelike depression of the testa (Figs. 1, 3, 5). This is sometimes less conspicuous as in *H. marlothii* (Fig. 9) or very prominent as in *H. luticola* (Fig. 8). Several species have a broader depression at the distal end (Figs. 2, 4, 11, 13, 14) or the seeds are merely truncate (Figs. 6, 7, 10).

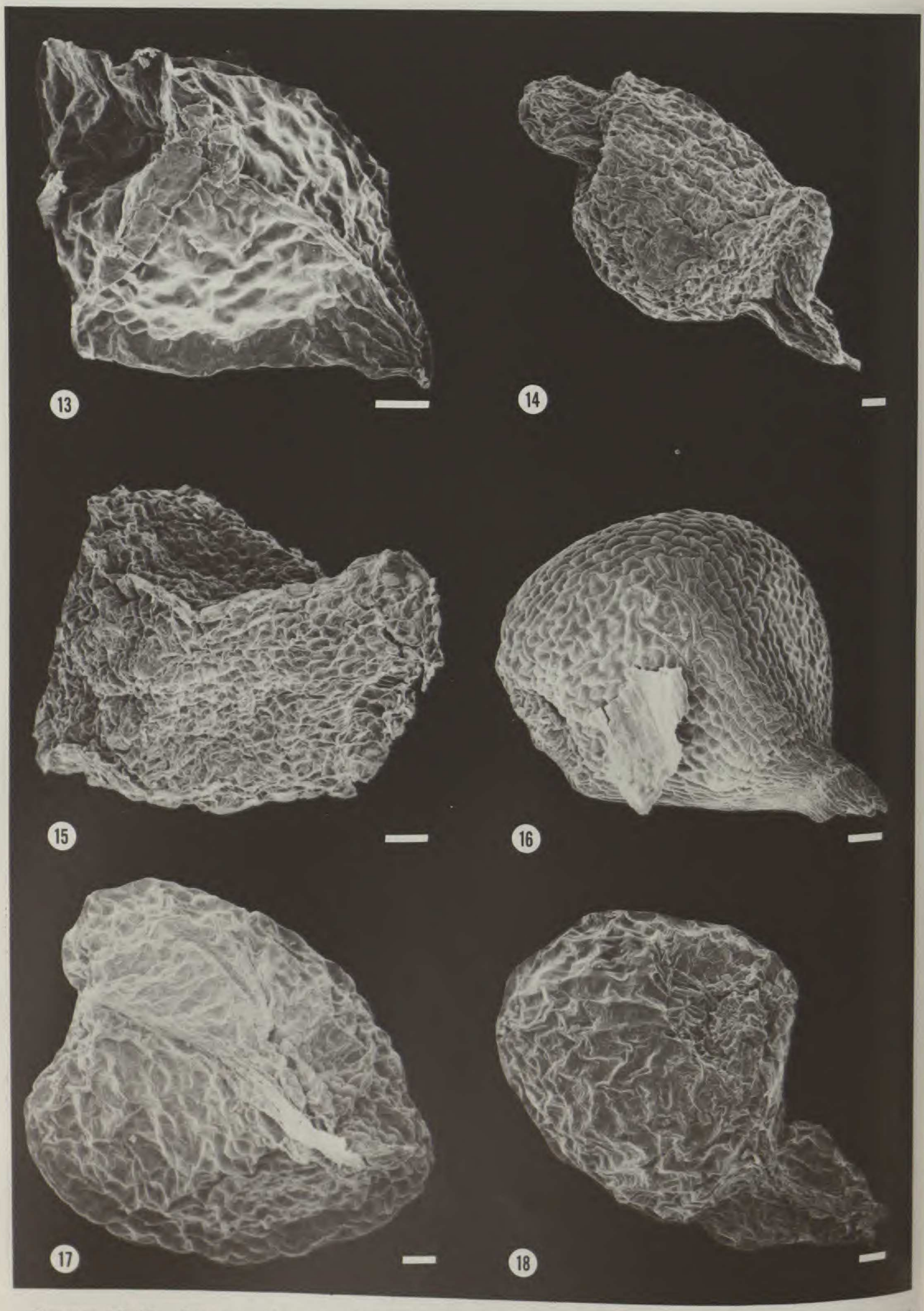
The raphe is often conspicuous and appears as



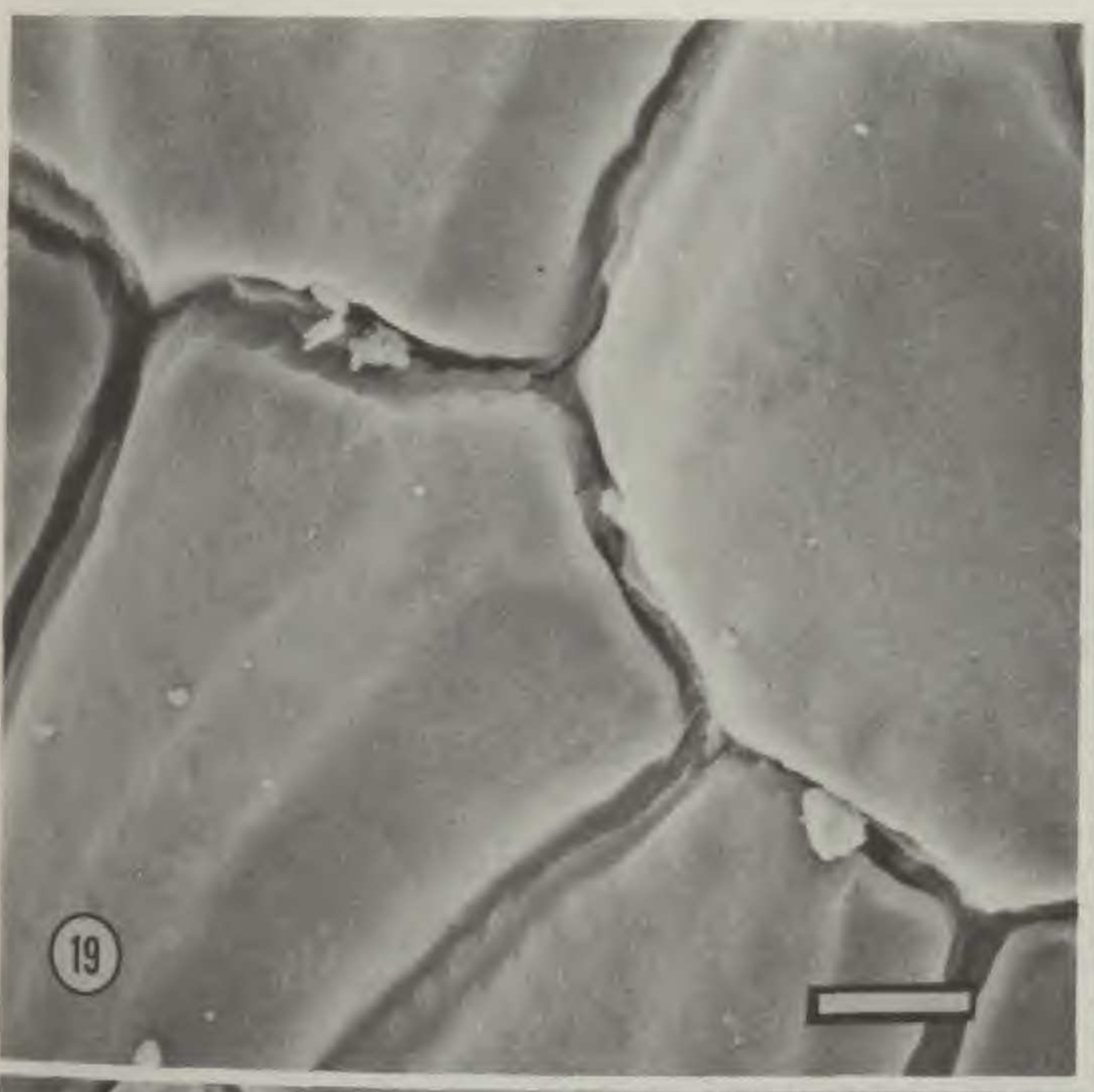
FIGURES 1–6. Scanning electron micrographs of seeds of *Hesperantha* species (Figs. 1, 2, sect. *Concentrica*; 3, 4, sect. *Imbricata*; 5, 6, sect. *Hesperantha*).—1. *H. erecta*.—2. *H. fibrosa*.—3. *H. purpurea*.—4. *H. bachmannii*.—5. *H. falcata*.—6. *H. spicata*. White bar = 100 μm.

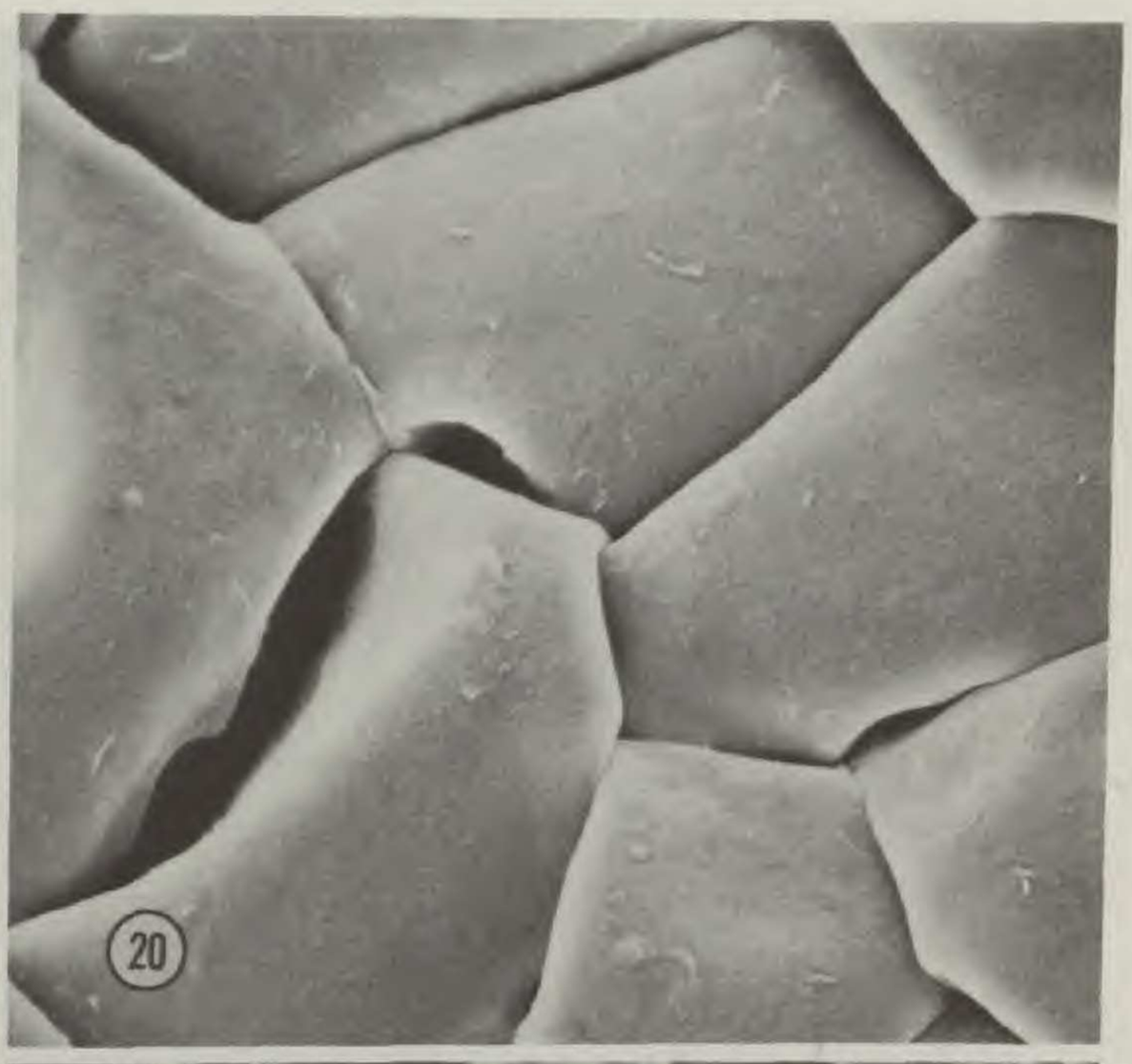


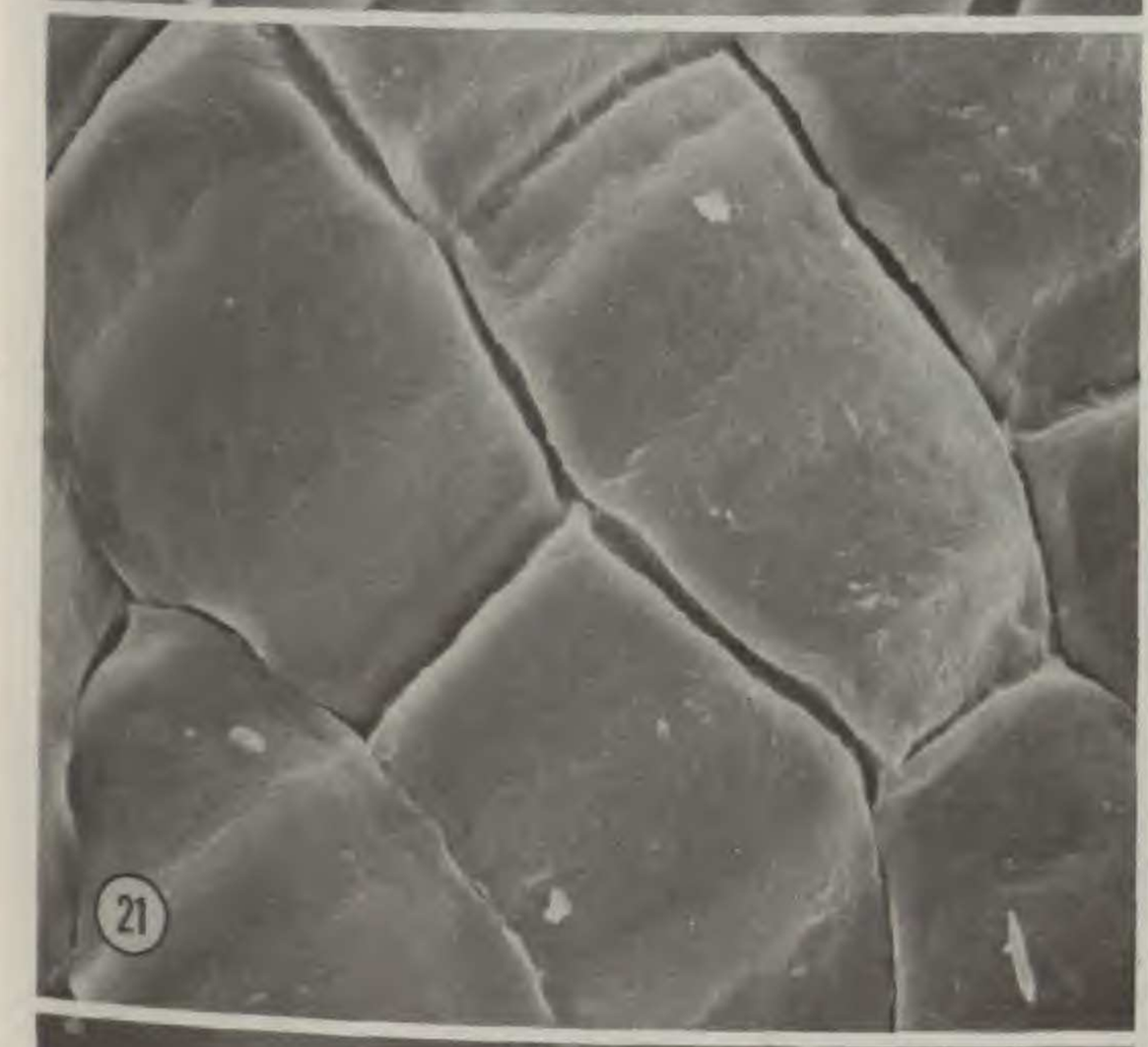
FIGURES 7–12. Scanning electron micrographs of seeds of species of *Hesperantha* (Figs. 7, 8, sect. *Hesperantha*; 9–12, sect. *Radiata*).—7. *H. cedarmontana*.—8. *H. luticola*.—9. *H. marlothii* (population 1).—10. *H. marlothii* (population 2).—11. *H. radiata*.—12. *H. brevifolia*. White bar = 100 μm.

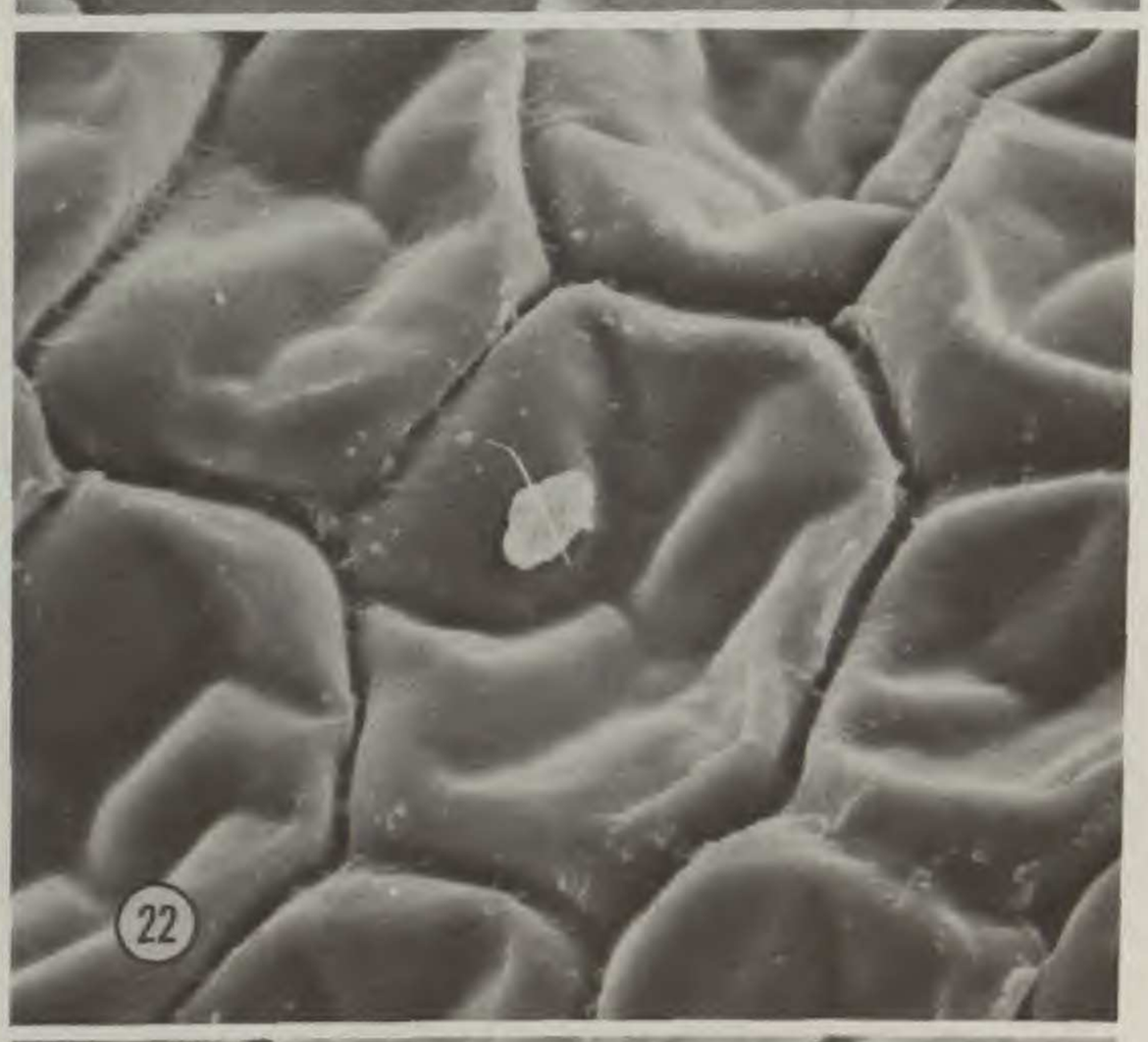


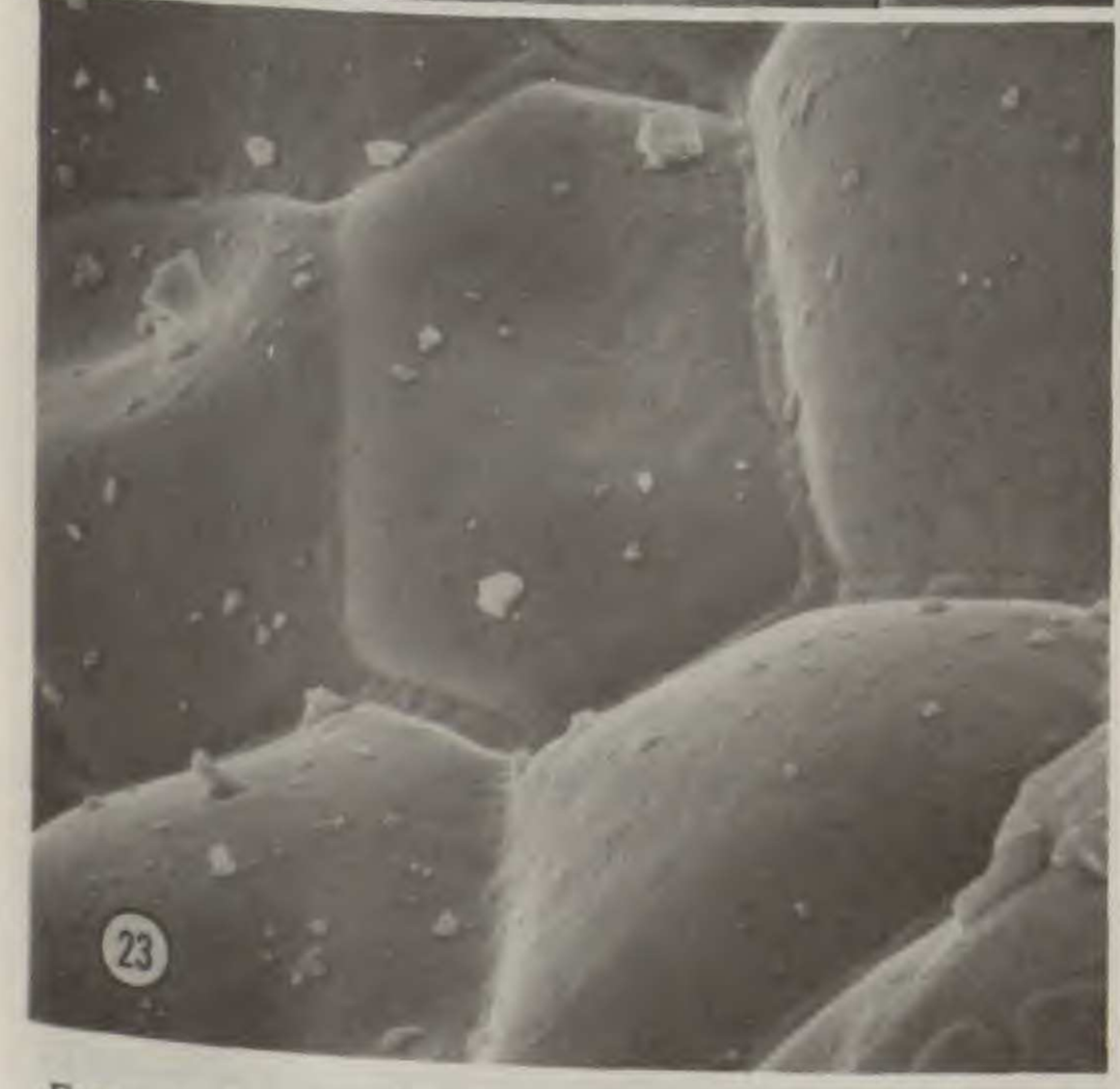
FIGURES 13–18. Scanning electron micrographs of seeds of species of *Hesperantha* sections *Radiata* and *Geissorhiza*.—13. *H. muirii*.—14,15. *H. elsiae*.—16. *G. humilis*.—17,18. *G. burchellii*. White bar = 100 μm.

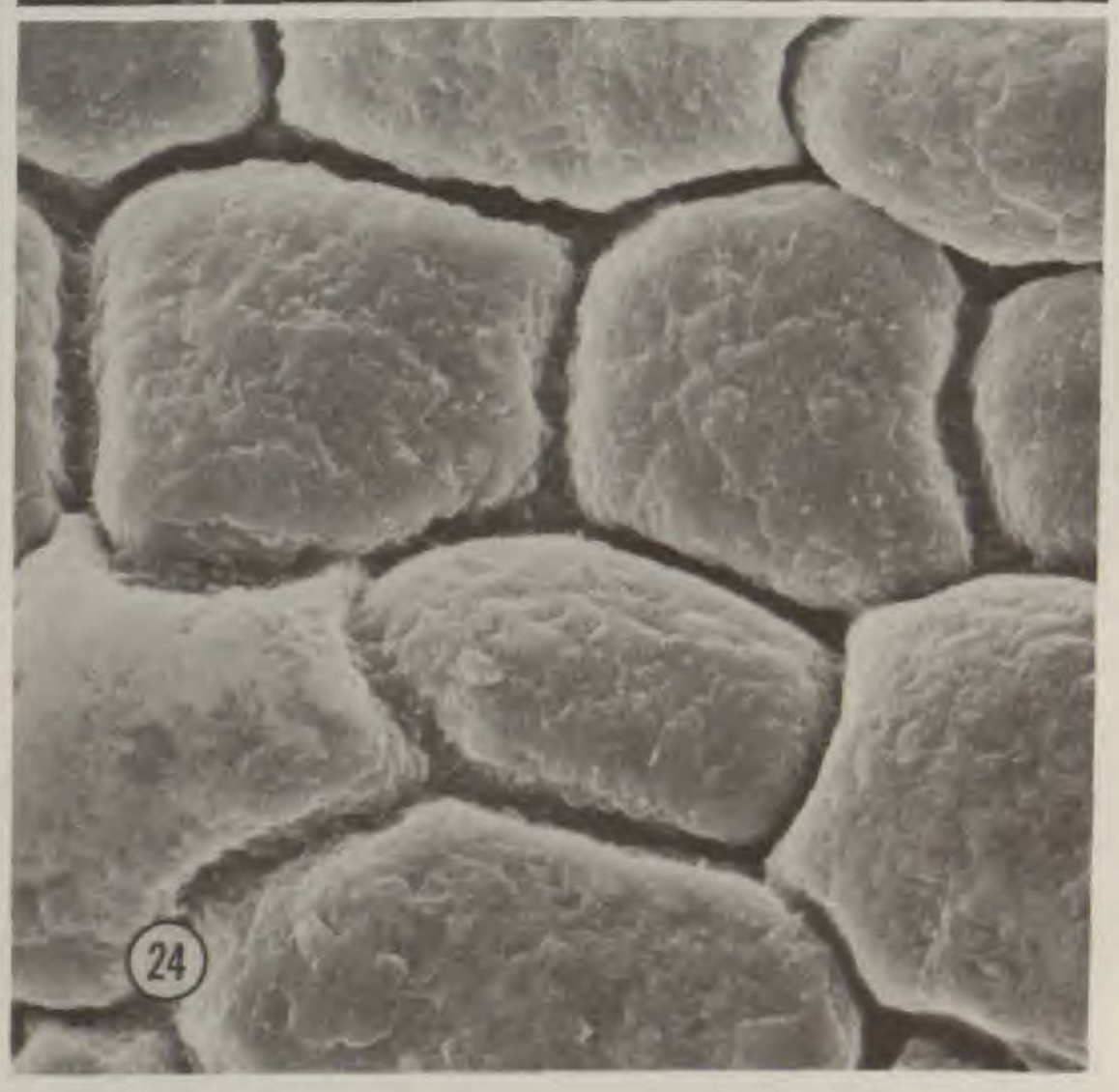




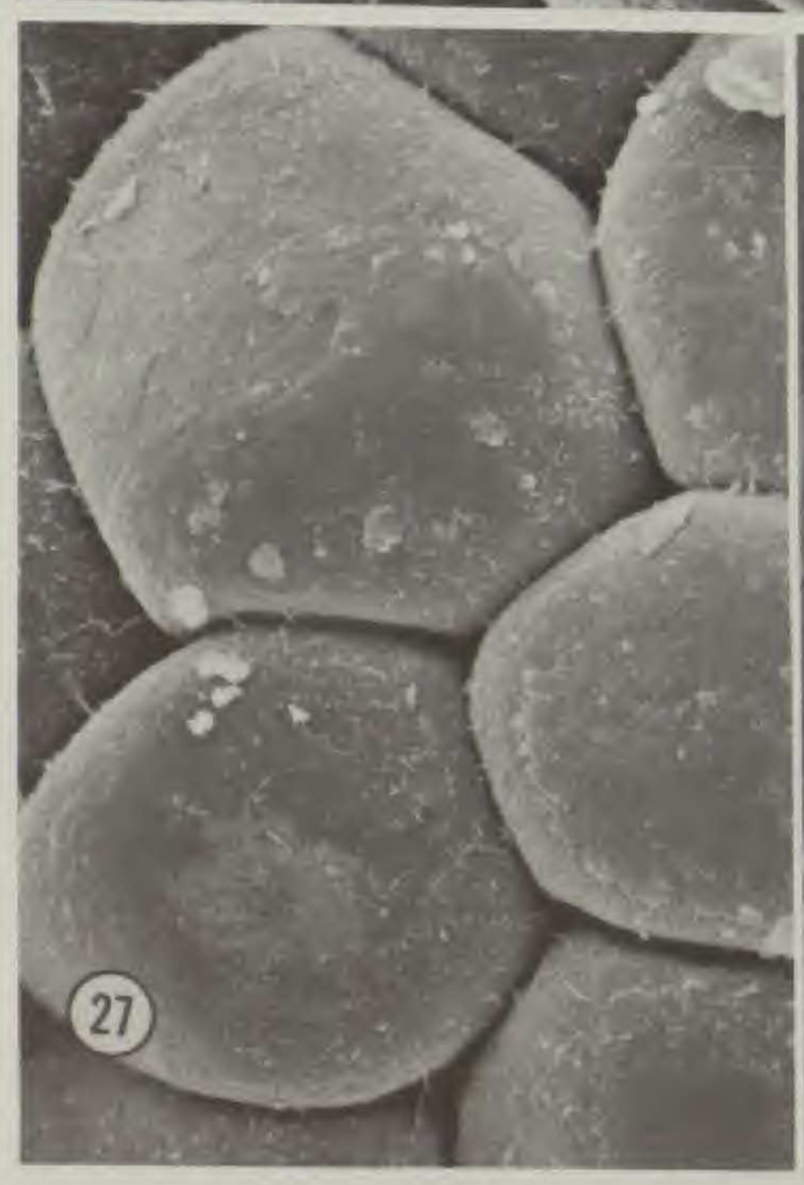








FIGURES 19–24. Scanning electron micrographs of epidermal cell surfaces of seeds of species of *Hesperantha* and *Geissorhiza*.—19. *H. erecta*.—20. *H. purpurea*.—21,22. *H. radiata*.—23. *G. heterostyla*.—24. *G. humilis*. White bar = 10 μm. Scale same for all Figures.



FIGURES 25–29. Scanning electron micrographs of epidermal cell surfaces of seeds of species of *Hesperantha*.—25. *H. cedarmontana*.—26. *H. spicata*.—27. *H. luticola*.—28. *H. brevifolia*.—29. *H. elsiae*. White bar = 10 μm.

a flat or raised area of the testa where the epidermal cells are elongated along the longitudinal axis of the seed (e.g., Figs. 1, 3, 6, 7). The species of *Geissorhiza* sampled have seeds with similar raphe and distal depressions (Figs. 16, 18).

Size. Most species of *Hesperantha* have relatively small seeds typically from 0.8 to 1.5 mm long. The seeds of *Geissorhiza* species examined also have a similar size range. Four species, *H. montigena* (sect. *Concentrica*), *H. bachmannii* (sect. *Imbricata*), *H. marlothii* (sect. *Radiata*) (Fig. 10), and *H. luticola* (sect. *Hesperantha*) (Fig. 8), have larger seeds, ranging from 1.3 to 2 mm long or to 2.5 mm long in one of the two populations of *H. marlothii* studied (population 1). In contrast, three species of sect. *Radiata*, *H. brevifolia* (Fig. 12), *H. muirii* (Fig. 13), and *H. elsiae* (Figs. 14, 15), have particularly small seeds, 0.5–0.7(–0.8) mm long.

Color. The seeds of both *Hesperantha* and *Geissorhiza* are light to dark brown except those of *H. flexuosa*, *H. radiata*, and *H. luticola*, each in a different section, which are reddish brown. The seeds of most species are moderately lustrous but some are much more so, such as *H. bachmannii* (sect. *Imbricata*) and *H. marlothii*

(population 1) (sect. *Radiata*). Seeds of *G. heterostyla* are similarly lustrous. Only *H. fibrosa* of sect. *Concentrica* and *H. luticola* of sect. *Hesperantha* have an unusually dull seed coat surface. The whitish color with a brown background of the seeds of *H. spicata* is a unique feature among the species sampled.

Surface morphology. The seed surfaces of both *Hesperantha* seeds and of those species of *Geissorhiza* sampled are composed of variable shaped epidermal cells (Figs. 19–29). Most cells are more or less isodiametric, but on ridges, wings, or contorted areas, the cell shape is usually altered (e.g., Fig. 20). The exposed periclinal cell wall is typically flat (Fig. 19) to slightly convex (Fig. 23). They are also often modified over parts of the seed surface to undulate (Fig. 21), convex (Fig. 22), irregular (Figs. 28, 29), or more spherical (Fig. 27). These modifications are either unique to one species such as the more spherical cells of *H. luticola* or are distributed sporadically in several sections, such as the three other types mentioned. The epidermal cell boundaries are distinct and fairly uniform among species of *Hesperantha* (Figs. 19, 21, 22, 25, 26) and appear similar to those of *Geissorhiza* (Figs. 23, 24). The boundaries are occasionally obscured by portions of the exposed periclinal walls that overlap (Fig. 20). Sometimes the boundaries are in full view but are not conspicuous (Figs. 28, 29). All three of these modifications appear to be minor and may be linked to the wrinkling or contortion of the testa surface as a result of packaging or desiccation.

Microsculpturing. The surface of the epidermal cells is generally smooth in both the *Hesperantha* and the *Geissorhiza* seeds surveyed. One species, *Geissorhiza humilis*, has an irregularly roughened surface. Within *Hesperantha* there are three species with roughened surfaces, *H. fibrosa* (sect. *Concentrica*), *H. cedarmontana*, and *H. spicata* (both sect. *Hesperantha*) (Figs. 25, 26). These roughened surfaces in *Hesperantha* are similar to one another but different from that of *Geissorhiza humilis* (Fig. 24). The similarity of the roughened surfaces of these three *Hesperantha* species suggests the possibility of a close relationship among them. Other species of *Hesperantha* have irregularly wrinkled cell surfaces (Fig. 29). This type of surface is closely linked to the contortion of the surface or portions of the surface in many species (e.g., Fig. 4). The very specialized seeds of *H. brevifolia* have a wrinkled cell surface unique among the species examined (Fig. 28).

Discussion

The basic seed shape in *Hesperantha* seems to be turbinate to more or less globose with a persistent funiculus and an epidermis of isodiametric cells with unwrinkled surfaces. A more globose shape may be due to either looser packing of the seeds in the capsule or a relatively simple modification that has occured several times independently. In any case this variation apparently has nothing to contribute to our understanding of species relationships.

There appear to be no seed characters restricted to *Hesperantha* and none have been identified that differentiate *Hesperantha* from *Geissorhiza*. Seeds of certain species such as *H. marlothii* (population 2) are virtually indistinguishable from those of some species of *Geissorhiza*. Moreover, there is limited variation among species of *Hesperantha*. The most conspicuous variations, like contorted and wrinkled seed coats, appear to be relatively minor changes and may be a consequence of the density of seed packing in the capsules or to desiccation or a combination of the two.

Wrinkled seed coats and globose seed shape have a sporadic distribution in the various sections of *Hesperantha* as well as in *Geissorhiza*, in the case of wrinkled seed coats, and they presumably have no taxonomic utility. Modifications that are apparently consistently reproduced (as far as it is possible to judge from the sampling), such as triangular seeds in *H. marlothii* (population 1), oddly wrinkled surfaces of the epidermal cells of *H. brevifolia*, or the more spherical epidermal cells and large seeds of *H. luticola*, appear restricted to only one species or form, and thus are also not useful in determining species relationships. The only exception to this is in sect. *Radiata*, where seeds with irregular shapes, strongly wrinkled or crumpled surfaces, a tendency for small size, and dual tails and/or wings support the belief in the close relationship of *H. radiata*, *H. muirii*, *H. brevifolia*, and *H. elsiae* based on gross morphology. *Hesperantha juncifolia* and *H. longicollis*, the other species of the section, were not available for study, while *H. marlothii*, evidently closely allied to *H. radiata* (Goldblatt, 1984), does not have this distinctive seed type.

The similarity between the seeds of *H. fibrosa* (sect. *Concentrica*) and *H. cedarmontana* and *H.*

spicata (sect. *Hesperantha*), all of which have seeds with narrow wings, little or no contortion of the epidermal cells, and roughened cell surfaces, in contrast seems fortuitous as there seems to be no support from gross morphology to suggest that *H. fibrosa* may be allied to the species of sect. *Hesperantha* with these same characteristics.

From the relatively small sample of 17 species examined here, it appears that the main pattern of evolution in seed structure in *Hesperantha* has been one of change from a basic turbinate shape with uncontorted, smooth surfaced epidermal cells to increasing compression and a triangular or more or less irregularly angular shape (perhaps a result of dense packing within the capsule) sometimes accompanied by wrinkling and crumpling of the epidermal cells, and the development of dual tails and wings. This is most marked within sect. *Radiata* (but not in *H. marlothii* of this section), where these modifications are accompanied by reduction in seed size. However, narrow wings are also developed within sections *Hesperantha* (*H. spicata* and *H. cedarmontana*) and *Concentrica* (only in *H. fibrosa* of the species examined) but in both of these groups without accompanying crumpling of the epidermal cells, which have distinctive rough surfaces, apparently developed coincidentally.

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